



Predicting the location of northern goshawk nests: modeling the spatial dependency between nest locations and forest structure

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Abstract

Northern goshawks interact with each other and their environment in a spatially dependent manner. However, finding the location of active goshawk nests (e.g. where eggs are laid) in a given year is difficult due to the secretive nature of the hawks in their forest environment, their annually variable attempts at nesting, and the extent of the area within a home range where they will nest. We used a Gibbsian pairwise potential model to describe the spatial dependency (1) among nest locations influenced by territoriality and (2) between nest locations and the environment for a large population of goshawks on the Kaibab National Forest's (NNF) North Kaibab Ranger District (NKRd). Nest locations in a given year were regularly distributed at a minimum distance of 1.6 km between active nests; however, as the spatial scale increased (i.e. as distance between the nests increased), the degree of regularity decreased. Important forest predictors for nest locations included canopy closure, total basal area, proportion of basal area in ponderosa pine, spruce, fir, and aspen, maximum height of the understory vegetation, and presence/absence of seedlings and saplings. The probability of an occurrence of an active nest within a 10-m × 10-m area was modeled using logistic regression. Spatial analysis, using nest spacing and habitat variables, indicated that potential active nest locations were abundant and randomly distributed throughout the NKRd. This supports the supposition that the availability of locations with high potential for nests is not limiting the goshawk population on the study area. Instead, territoriality, and what appear to be non-compressible territories, sets the upper limit to the nesting population. Ultimate choice of nest location was probably constrained by the availability of high potential locations within spaces defined by neighboring territories. Overall territory density, on the other hand, may reflect the abundance, quality, and accessibility of prey on the study area. This model can be used to evaluate the influence of forest management activities on the nesting goshawk population on the NKRd. The modeling technique described in this paper may be applied to other study areas, where vertebrate densities and the spatial resolution of habitat data may be less or greater than on this study, provided that new point process and pairwise potential models are developed for each area.

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1. Introduction

The northern goshawk (*Accipiter gentilis*; hereafter goshawk) has been the focus of intensive research for the past decade (Block et al., 1994; Kennedy, 1997; Peck, 2000) because of suspected population declines

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38 due to loss of habitat (Reynolds, 1983, 1989; Kenward
39 and Widén, 1989; Speiser and Bosakowski, 1984;
40 Crocker-Bedford, 1990; Widén, 1997) and changes in
41 forest structure (Reynolds et al., 1992), both result-
42 ing from forest management. Many goshawk studies
43 in North America and Europe have focused on the
44 hawks' habitat use, food habits, movements, distri-
45 bution, demographics, and diets (Block et al., 1994);
46 however, no studies have attempted to use spatially
47 explicit models to describe simultaneously the spatial
48 dynamics among goshawks and between goshawks
49 and their environment. Although some researchers
50 (Clark et al., 1993; Baker et al., 1995; Augustin et al.,
51 1996; Ripple et al., 1997; van Manen and Pelton,
52 1997; Carroll et al., 1999; Dettmers and Bart, 1999;
53 Mladenoff et al., 1999; Swindle et al., 1999; Thome
54 et al., 1999; Pearce and Ferrier, 2000; Mitchell et al.,
55 2001; Finn et al., 2002) have used spatial modeling
56 to explore wildlife-habitat relationships, few (Reich
57 et al., 2000; Peres-Neto et al., 2001; Austin, 2002)
58 have recognized their value in exploring these mani-
59 fold spatial dependencies.

60 Goshawks interact with conspecifics (members of
61 the same species) and their habitat in a spatially depen-
62 dent manner (Widén, 1985; Selås, 1997; Reynolds and
63 Joy, 1998). By first describing the spatial distribution
64 among active goshawk nests (i.e. nests in which eggs
65 are laid) within a goshawk population and then mod-
66 eling the interaction between nest locations and forest
67 structure, it may be possible to predict the location of
68 active nests in a given year. Locating active nests is
69 extremely difficult due to the secretive nature of the
70 birds and their annually variable attempts at nesting
71 (Reynolds and Joy, 1998), nest concealment, and the
72 size of the area within their home ranges where they
73 will nest.

74 Many bird species, such as the goshawk, attempt to
75 exclude conspecifics from all or a part of their terri-
76 tory. Territoriality, in most cases, is an effort to secure
77 resources, such as food and a mate, against their use by
78 others, thereby increasing an individual bird's fitness
79 (Ricklefs, 1973). Such behavior tends to space nests
80 evenly throughout their habitat. Thus, the size of an in-
81 dividual territory tends to vary from species to species,
82 and within species from habitat to habitat depending
83 on the availability of resources. Spatial point process
84 models that are commonly used to model such pat-
85 terns include the Markov point process and Gibbs dis-

tribution. Ripley and Kelly (1977) first introduced the 86
Markov point process model, while the Gibbs model 87
has a longer history in statistical physics (Preston, 88
1977). These models provide the basis for describing 89
complex spatial patterns and have been used widely 90
for modeling regular spatial patterns (Ripley, 1977; 91
Ogata and Tanemura, 1981, 1984). Taking into con- 92
sideration a species' spatial pattern incorporates both 93
biologically and ecologically meaningful information 94
into the modeling process, as a close relationship ex- 95
ists between the abundance of an individual species 96
and its spatial distribution. 97

Intra-specific competition (i.e. territoriality) is a 98
complex biological phenomenon. Therefore, any spa- 99
tial point process model developed to describe this 100
spatial relationship is necessarily an approximation 101
of the true process. Such models are limited by the 102
availability of sufficient data to estimate reliably all 103
the parameters required by the models. Even if such 104
models could be developed, they may be of limited 105
value unless (1) the corresponding data required to 106
implement the model were available and (2) the model 107
was based on variables that were easily obtained in 108
the field. However, models such as the Markov point 109
processes and Gibbs distributions have been found to 110
perform adequately in such situations. These mod- 111
els are based on simple assumptions relating to how 112
points interact in a pairwise fashion (such as, the 113
influence between pairs of points depends on their 114
relative, not the absolute, positions) and are relatively 115
easy to fit. 116

Since their introduction, much attention has focused 117
on a special case of the Markov and Gibbs mod- 118
els, the pairwise interaction model, in which a set of 119
points (e.g. nests) are considered to interact in a pair- 120
wise fashion (Strauss, 1975; Besag et al., 1982; Diggle 121
et al., 1987; Ripley, 1990; Cressie, 1991, pp. 674–678; 122
Diggle et al., 1992). "Competitive" intra-specific inter- 123
actions may therefore be described by the pairwise po- 124
tential function of either model. In addition, the Gibb- 125
sian pairwise potential model may be expanded by in- 126
cluding environmental variables to identify potential 127
habitat for a species in a landscape (Reich et al., 1997). 128
As a result, the model performs similarly to other habi- 129
tat predicting techniques (e.g. generalized linear model 130
(GLM), generalized additive models (GAM), classifi- 131
cation and regression tree models). The model's ad- 132
vantage, however, is in its ability to simulate dynamic 133

134 and interactive ecological processes to achieve greater
135 ecological “reality” in predicting species occurrences.

136 In this paper, we fit a Gibbsian pairwise poten-
137 tial model to describe the spatial variability among
138 goshawk nests and their association with forest struc-
139 ture on the Kaibab National Forest’s (KNF) North
140 Kaibab Ranger District (NKR) in northern Ari-
141 zona. We also identify habitat that is more likely to
142 have nests by correlating the location of known nests
143 with environmental variables that account for the
144 coarse-scale variability (gradients) across the land-
145 scape. Finally, we explain how this modeling effort
146 may be applied to other vertebrate studies and study
147 areas.

148 2. Study area

149 The study area (1285 km²) included forests on the
150 NKR above 2182 m in elevation. This elevation was
151 chosen because it represented the lower elevation of
152 the distribution of forest; below this elevation forests
153 were dominated by shorter pinyon (*Pinus edulis*)–
154 juniper (*Juniperus* spp.) woodlands where goshawks
155 rarely nest (Squires and Reynolds, 1997; S.M. Joy,
156 personal observation). The study area comprises the
157 northern two-thirds of the Kaibab Plateau in northern
158 Arizona and is bounded by the Grand Canyon Na-
159 tional Park to the south, steep slopes to the east, and
160 gentle slopes to the north and west that descend to
161 a shrub-steppe plain. Six vegetation classes dominate
162 the study area (Fig. 1; Joy et al., 2003): (1) pinyon–
163 juniper woodlands (106 km², 8% of study area) occur
164 at lower elevations (2182–2250 m) and mix with pon-
165 derosa pine (*Pinus ponderosa*) at transitional zones;
166 (2) ponderosa pine (704 km², 55%) occurs between
167 2250 and 2550 m; (3) mixed-conifer, comprised of
168 ponderosa pine, white fir (*Abies concolor*), Douglas-fir
169 (*Pseudotsuga mensiesii*), and quaking aspen (*Populus*
170 *tremuloies*) (145 km², 11%), occurs between 2550 and
171 2650 m elevation; (4) spruce (*Picea pungens*, *Picea*
172 *englemannii*)-dominated mixes (130 km², 10%), pri-
173 marily with subalpine fir (*Abies lasiocarpa*), occurs
174 above 2650 m elevation; (5) deciduous (quaking aspen,
175 Gamble’s oak (*Quercus gambeli*))-dominated mixes
176 (112 km², 9%) occur throughout the forest and are
177 common where extensive disturbance has occurred
178 (Fig. 1); and (6) openings (90 km², 7%) that contain

179 grasses and herbaceous vegetation include a series of
180 long, narrow meadows and various smaller gaps in the
181 canopy which are scattered throughout the forest.

182 Nearly all of the KNF has been altered by some
183 form of management during the past 100 years
184 (Pearson, 1950; Burnett, 1991). By the early-1900s
185 livestock grazing was common and fire suppression
186 had been established. A long-term policy of fire exclu-
187 sion has resulted in large numbers of shade-tolerant
188 seedlings and saplings throughout the forest creating
189 fuels and a closing-in of the historically more-open
190 understory (Weaver, 1951). Organized tree harvests
191 in the form of sanitation cuts and single-tree selection
192 began in the 1920s. These harvest regimes continued,
193 along with occasional, small (0.1 km²) clearcuts in
194 the mixed-conifer zone, until the late-1970s. Intensive
195 forest management at the stand level (shelterwood,
196 seed, salvage, removal, and thinning cuts) began in
197 the 1980s and continued until 1991, when the NKR
198 implemented forest management prescriptions de-
199 signed to enhance the habitat of goshawks and their
200 prey (Reynolds et al., 1992).

201 The NKR receives about 67.5 cm of precipitation
202 annually, with winter snowpacks of 2.5–3.0 m (White
203 and Vankat, 1993). A drought period typically occurs
204 in May and June, followed by mid- to late-summer
205 thunderstorms and heavy showers.

206 3. Methods

207 3.1. The data

208 The data layers used to model spatial dependencies
209 among goshawks and their environment included the
210 location of active nests, field measurement, Landsat
211 Thematic Mapper (TM) imagery, and GIS-derived to-
212 pographic variables. Nest locations were used to de-
213 scribe the spatial distribution of nests; whereas, the
214 field measurements, Landsat imagery, and topographic
215 variables were used to model forest composition and
216 structure to a 10-m spatial resolution.

217 3.1.1. Goshawk nest locations

218 Searches for active goshawk nests began in 1991
219 and continued through 1998. Nest searches began in
220 April and ended after the post-fledging period (mid-
221 August). Each year, the overall search area on the

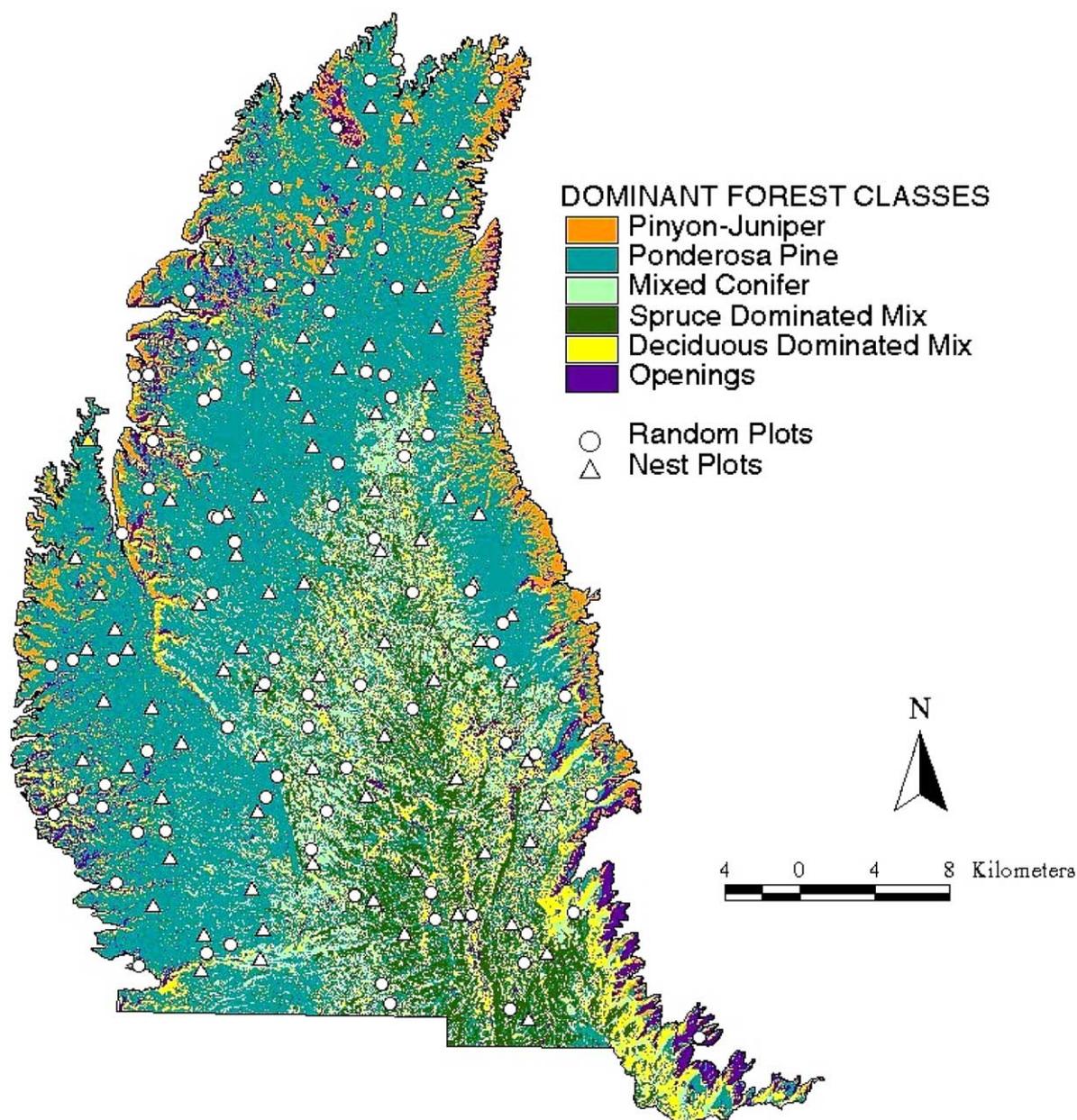


Fig. 1. Distribution and arrangement of nest plots (△) and random plots (○) used to model forest structure displayed among dominant vegetation classes on the North Kaibab Ranger District, Kaibab National Forest, Arizona.

222 NKRD was expanded to include more territories. Nests
 223 were found by (1) searching on foot (Reynolds, 1982),
 224 (2) systematically broadcasting goshawk vocalizations
 225 from predetermined stations on transects (Kennedy
 226 and Stahlecker, 1993; Joy et al., 1994), and (3) visiting

active nests found in prior years of the study. When the
 227 status of a previously-active nest remained unknown,
 228 searches of 16 and 24 km² areas around that nest were
 229 carried out on foot or by broadcasting, respectively,
 230 to locate an alternate active nest within the territory.
 231

232 Goshawks may use more than one nest within their territories among breeding years (Reynolds and Wight, 1978; Reynolds et al., 1994; Reynolds and Joy, 1998). A “territory” (approximately 1.5 km radius) is the area used and defended by a single pair of goshawks during the nesting season and may contain one or more alternate nest trees (Reynolds et al., 1994). At each active nest, adults and juveniles were captured and banded with a USDI Fish and Wildlife Service aluminum leg band and an anodized aluminum colored leg band, the latter marked with unique two-character alpha-numeric codes readable at up to 50–80 m with 20–40 power spotting scopes. Identifying the individual goshawks allowed us to correctly associate new nests with individual territories. On the study area, territoriality is maintained even in non-breeding years by marked individuals who continue to defend their territory (Reynolds et al., 1994).

250 3.1.2. Field data

251 Models of forest structure were based on the spatial interpolation of habitat attributes at both active nests sites and randomly selected sites (Fig. 1):

- 254 • *Goshawk nest plots.* We measured the forest vegetation immediately surrounding the nest tree at one nest within each of 92 goshawk territories studied through 1998. In territories containing multiple active alternate nests that had been active since 1991, we randomly selected one alternate at which to measure the forest characteristics. At single-nest territories, we measured the vegetation at that nest tree.
- 263 • *Randomly located plots.* To describe the spatial/structural variability on the NKR D, we located 85 random plots throughout the study area. We placed no constraints on the location of random plots (i.e. they were placed irrespective of territories and nests), because we considered all habitat to be potentially available to goshawks for nest site use.

270 3.1.3. GIS and Landsat TM data

271 The GIS database consisted of four topographic variables (elevation, slope, aspect, and landform), six bands (1–5, and 7) of Landsat TM data (1997; 22 June; Path 37, Row 35), and seven variables representing stand structure (percent canopy closure; total basal area; proportions of (a) ponderosa pine, (b)

spruce/fir, and (c) aspen in the total basal area; maximum height of the understory vegetation; and the presence of seedlings or saplings). All habitat-related variables were believed to be important to goshawk nest tree selection. Elevation was obtained from USGS digital elevation models (DEM) and used to derive aspect and slope. The DEM was also used to calculate a landform index (McNab, 1989), which expresses surface shape as a measure of surface concavity or convexity (computed as the mean slope gradient from the original cell to adjacent cells in 4 directions), a continuous variable. Grid coverages for elevation, slope, aspect, and landform were resampled to 10 m, corresponding to the spatial resolution of the field data (below). Grid coverages representing forest structure were developed by spatially interpolating the random and nest-based field data to a 10-m spatial resolution using trend surface models and regression trees (Joy, 2002, pp. 46–95). Landsat bands 1–5 and 7, and topographic data were used as predictor variables. All grid manipulations were performed in ArcView® (ESRI, 1998).

3.2. Field measurements

299 Because the spatial variability in forest structure can vary at scales smaller than those determined by the spatial resolution of Landsat TM imagery (i.e. <30 m), we designed our field sampling to classify forest structure to a 10-m spatial resolution. Sample plots consisted of a cluster of nine 10-m × 10-m subplots that corresponded to a 30-m × 30-m pixel on our Landsat TM imagery, the location of which was verified using a Trimble Navigation Pathfinder™ Asset Surveyor Global Positioning System (estimated accuracy = 1–3 m). Field measurements were collected during August and September of 1997. Each plot was established in a north–south, east–west fashion with the coordinate systematically assigned to either the center (nest tree plot) or lower left corner (random plots) of the plot. Vegetative characteristics were recorded on each of the nine 10-m × 10-m subplots and included canopy closure (measured with a concave, spherical densiometer; Lemmon, 1956, 1957), overstory species, total basal area by species (measured with a 20 factor prism), height of the understory vegetation, and the presence of seedlings and saplings.

3.3. Spatial distribution of active goshawk nests

Territoriality (i.e. behavior related to the defense of a specified area against intruders) is assumed to strongly influence the spatial distribution of nests among breeding pairs of goshawks across the landscape. Therefore, intra-specific behavior such as this is a necessary component of any habitat model involving breeding birds. To model the distribution of active goshawk nests, we selected a large (528 km²) rectangular region within the NKRD. A rectangular region was selected to simplify the algorithm required to adjust for edge effects, while the shape of the rectangular was selected to include as many nests as possible. The spatial location of all active nests in 1998 within the rectangular region *B* (Fig. 2) was assumed to represent the spatial relationship between active goshawk nests and forest structure when the population is at or near full occupancy because, in 1998, active nests attained the most continuous spacing (i.e. fewest gaps due to non-nesting territorial pairs or individuals) among all the breeding years studied (Fig. 3).

Using the spatial location of each nest in the rectangular region *B*, a Monte Carlo test (Besag and Diggle, 1977) based on the Cramér–von Mises type statistic (Cressie, 1991, p. 642)

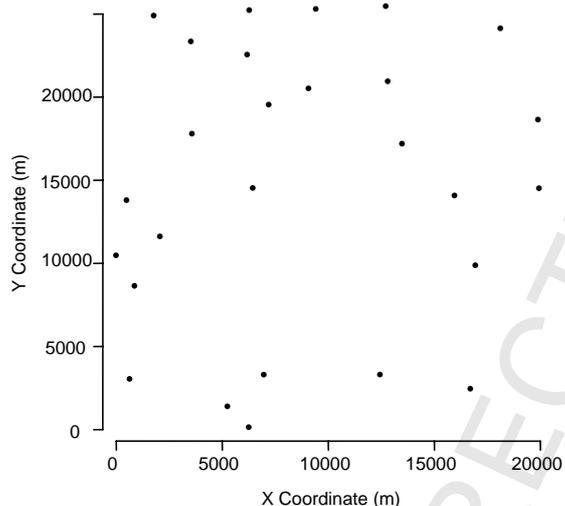


Fig. 2. Bounded region (*B*) showing the relative location of 27 active northern goshawk nests from 1998 used to model the spatial relationship between active nests and forest structure.

$$k = \int_0^H [\hat{K}(h)^{1/2} - \pi^{1/2}h]^2 dh \quad (1) \quad 349$$

was used to test the null hypothesis of complete spatial randomness (CSR); i.e. whether the arrangement of nests within a circular region of radius *H* does not differ significantly from that expected under the assumption of CSR. This was done at 14 spatial scales ranging from 2 to 16 km in increments of 1 km by simulating values of the test statistic under CSR and comparing them to the corresponding statistic calculated from the observed pattern of active goshawk nests. For each simulation, we calculated the empirical *K*-function, $\hat{K}_i(h)$ (Ripley, 1977), corrected for edge effect (Cressie, 1991, p. 616), and the Cramér–von Mises statistic *k*. The significance (*P*-value) of the test was calculated as $\hat{p} = (R + 1 - r)/R$, where *R* is the number of simulations, and *r* is the rank of the test statistic associated with the observed point pattern. A small *P*-value supports the alternative hypothesis of a non-random spatial pattern. All tests were based on 200 realizations of a spatial Poisson process to allow for the calculation of a *P*-value to the nearest 1%.

Traditional nearest neighbor statistics, which are often used to test nest spacing (e.g. Newton et al., 1977), assume that the nearest neighbors are independent (Cressie, 1991, pp. 603–606). If applied to mapped data sets such as nests, however, the nearest neighbor measurements are not independent, and one would tend to reject the null hypothesis of CSR too often (Cressie, 1991, p. 610). In contrast, the *K*-function and the Cramer–von Mises goodness-of-fit test do not assume that distance measurements are independent. Furthermore, they use information on many spatial scales because they are based on squared distances to the first, . . . , *k*th nearest neighbors.

3.4. Gibbsian pairwise potential model

The Gibbsian pairwise potential model is a Markov point process, a flexible class of models in that they simulate both regular (inhibition) and aggregated (contagious) patterns. The primary use of such models has been in the study of regular point patterns, such as those exhibited by the goshawk (Reynolds and Joy, 1998; Widén, 1985), other accipiters (Newton et al.,



Fig. 3. The location of active northern goshawk nests between 1991 and 1998 on the North Kaibab Ranger District, Kaibab National Forest, Arizona.

393 1977), as well as other raptors (Cade, 1960; Ratcliffe,
394 1962; Newton, 1979).

395 The most extreme form of spatial regularity results
396 from the direct exclusion from a given area, whether
397 by complete occupancy, allelopathy, or territoriality.
398 Models that describe such phenomenon are termed
399 hard-core models. Every individual in the population
400 has a circular neighborhood within which no other
401 individual can exist. For biological populations that
402 display plasticity of size and shape, the hard-core
403 model may be too extreme. As an alternative, a
404 soft-core model with fixed-range interactions may
405 be used. Soft-core models are less extreme, in that
406 within a given neighborhood of radius R , inhibition
407 is not complete, and a competitive effect (i.e. terri-
408 toriality) is experienced. The degree of territoriality

may or may not be a function of the distance between 409
individual pairs (h). 410

3.4.1. Potential energy of goshawk nests 411

The location of all N goshawk nests within the 412
bounded region B were assigned coordinates $X =$ 413
 $\{X_i = (x_i, y_i) \in B, i = 1, \dots, N\}$. To model the spa- 414
tial distribution and association of individual territorial 415
goshawk pairs (i.e. nests), we assumed that the terri- 416
torial influence between pairs depended on the rela- 417
tive, and not the absolute position of nests. This as- 418
sumption implies a homogeneous environment. The 419
territorial interaction, or potential energy, Ψ , can be 420
modeled as a function of the Euclidean distance $h_{ij} =$ 421
 $\|X_i - X_j\|$ between pairs of nests in which the terri- 422
torial influence between individual pairs decreases 423

424 with increasing distance. Thus, the total potential energy for the point process is defined as (Cressie, 1991, p. 677):

$$U_N(X) = \sum_{i < j}^N \Psi(h_{ij}), \quad (2)$$

428 where $U_N(X)$ can be thought of as the total energy required to add a nest to the point pattern. The observed point pattern of goshawk nests, therefore, can be regarded as being distributed according to a Gibbs canonical distribution:

$$f(x) = \frac{\exp[-U_N(X)]}{Z(\Psi; N)}, \quad (3)$$

434 where $Z(\Psi; N)$ is a normalizing constant where the joint probability density integrates to 1. If the normalizing constant exists, the point pattern is said to be stable. The sign and shape of the potential functions are determined by whether there is inhibition or attraction between nests. Positive values indicate inhibition, while negative values represent attraction. If no interactions exist between nests, the value of the potential function is zero. A strictly positive pairwise potential (i.e. inhibition process) always yields a stable process, while those with negative potential energy at some specified distances (i.e. contagious process) are generally unstable (Cressie, 1991, p. 678).

448 3.4.2. Model parameter estimation

449 Consider a family of parameterized pairwise potential functions $[\Psi_\theta(h); \theta \in \Theta]$. Given a finite set of points in a bounded region, B , the likelihood of the potential function $\Psi_\theta(h)$ is given by the Gibbs canonical distribution (Eq. (3)). The maximum likelihood estimate of θ is obtained by finding a $\hat{\theta}$ that maximizes Eq. (3). Maximization requires computing the normalizing constant $Z(\Psi; N)$, which is not usually available in closed form (i.e. where an explicit solution exists). Ogata and Tanemura (1981) use the cluster-expansion method of statistical mechanics (Ogata and Tanemura, 1981; Cressie, 1991, p. 682) to obtain an approximation of the normalizing constant, conditioned on the number of points in B :

$$Z(\Psi; N) = |B|^N \left(\frac{1 - a(\theta)}{|B|} \right)^{N(N-1)/2}, \quad (4)$$

where

$$a(\theta) = 2\pi \int_0^\infty h [1 - \exp(-\psi_\theta(h))] dh \quad (5)$$

466 is the second cluster integral, and $|B|$ is the area of the bounded region B . In their approximation, only pairwise interactions were considered; higher order interactions were assumed to be negligible. Cressie (1991, p. 683) points out that this approximation holds only for stable pair-potentials, and may not be valid for unstable pair-potentials that require higher-order interactions such as a Markov cluster process. Combining Eqs. (3) and (4) leads to the approximate log likelihood function:

$$\log L(\theta|X) = \sum_{i < j}^N \Psi_\theta(\|X_i - X_j\|) - \frac{1}{2} N(N-1) \log \left(1 - \frac{a(\theta)}{|B|} \right), \quad (6)$$

479 which can be solved using nonlinear optimization procedures.

481 To use this relationship in describing the spatial distribution and association of individual nests, one must be able to mathematically describe the interaction potentials of a spatial point pattern. Three parameterized potential functions proposed by Ogata and Tanemura (1981, 1985) are available to describe the interactions observed in the distribution of the goshawk nests:

$$\text{PF1 : } \Psi_\theta(h) = -\log[1 + (\alpha h - 1) e^{-\beta h^2}], \quad \theta = (\alpha, \beta), \alpha \geq 0, \beta > 0 \quad (7)$$

$$\text{PF2 : } \Psi_\theta(h) = -\log[1 + (\alpha - 1) e^{-\beta h^2}], \quad \theta = (\alpha, \beta), \alpha \geq 0, \beta > 0 \quad (8)$$

$$\text{PF3 : } \Psi_\theta(h) = \beta \left(\frac{\sigma}{h} \right)^{12} - \alpha \left(\frac{\sigma}{h} \right)^6, \quad \theta = (\alpha, \beta, \sigma), \beta > 0. \quad (9)$$

499 All three potential functions can model both repulsive and attractive forces. The parameter, α , controls the type of force between a pair of points, while β and σ are scaling parameters. The potential function PF1 represents a purely repulsive potential when $\alpha = 0$, and has both repulsive and attractive potentials when $\alpha > 0$. The potential function PF2 is repulsive when

506 $0 \leq \alpha < 1$, independent when $\alpha = 1$, and attractive
507 when $\alpha > 1$. The potential for PF3 is purely repulsive
508 when $\alpha < 0$, and attractive when $\alpha > 0$. The second
509 cluster integral, $a(\theta)$, for the three potential functions
510 are given by

$$511 \text{ PF1 : } a(\alpha, \beta) = \left(\frac{\pi}{\beta}\right) \left(\frac{1 - \alpha\sqrt{\pi/\beta}}{2}\right) \quad (10)$$

$$512 \text{ PF2 : } a(\alpha, \beta) = \frac{\pi(1 - \alpha)}{\beta} \quad (11)$$

$$514 \text{ PF3 : } a(\alpha, \beta, \sigma) \\ 515 = -\frac{\pi}{6}\beta^{1/6}\sigma^2 \sum_{k=0}^{\infty} \frac{1}{k!} \Gamma\left(\frac{6k-2}{12}\right) \alpha^k \beta^{-k/2}. \quad (12)$$

516 The pairwise potential models PF1–PF3 were fit to
517 the point data of the individual nests using a nonlin-
518 ear least squares procedure to obtain an estimate of
519 the parameter vector $\theta = (\alpha, \beta)$ or $\theta = (\alpha, \beta, \sigma)$ that
520 maximized the approximate log likelihood (Eq. (6)).
521 Akaike's (1977) AIC, was used to select the best
522 model among the three possible models (PF1–PF3).

523 3.5. Potential energy between nests and forest 524 structure

525 To include environmental heterogeneity in the
526 model, the total potential energy was redefined as
527 follows:

$$528 U_N(X) = \sum_{i < j}^N \Psi(h_{ij}) + \sum_{i=1}^N \phi(z_i), \quad (13)$$

529 where $\phi(z_i)$ is a measure of the interaction of individ-
530 ual nests with the environment (i.e. forest structure).
531 If we assume that the presence, or absence, of a nest
532 is correlated to a set of known environmental vari-
533 ables we can, for example, define the probability of
534 observing a goshawk nest at a given location as π . The
535 potential energy associated with this location can be
536 expressed as (Reich et al., 1997):

$$537 \phi(z) = \frac{1}{\pi} - 1 = f(\text{environmental variables}). \quad (14)$$

538 Large positive values indicate “poor” nest locations
539 while small values indicate “good” nest locations.
540 We define “good” nest locations as those with higher
541 probabilities of observing an active nest (see above).

542 “Good” locations as defined by forest structure, how-
543 ever, do not necessarily confer greater fitness on the
544 birds using those sites (Van Horne, 1983; Vickery
545 et al., 1992) because fitness (measured directly or
546 indirectly by survival and reproductive success) is
547 a function of, not only, habitat characteristics, but
548 also food resources and life history strategies used
549 throughout the home range (Newton et al., 1977;
550 Reynolds et al., 1992; Kostrzewa, 1996). Furthermore,
551 the presence of good habitat alone does not guarantee
552 that a nest will be present because the value of an
553 area as a nest location is dependent upon the arrange-
554 ment of both fine- and coarse-scale (i.e. landscape
555 scale) variability in the landscape (Ricklefs, 1987),
556 territoriality, and population density.

557 3.6. Modeling nest site suitability

558 To model the potential energy associated with forest
559 structure we used a multiple logistic regression model
560 (Hosmer and Lemeshow, 1989; Manly et al., 1993):

$$561 \pi = \frac{e^{\beta_0 + \beta_1 z_1 + \dots + \beta_k z_k}}{1 + e^{\beta_0 + \beta_1 z_1 + \dots + \beta_k z_k}}, \quad (15)$$

562 where π is the probability of observing a goshawk
563 nest, z_1, \dots, z_k are independent predictor variables,
564 and β_1, \dots, β_k are logistic coefficients. Independent
565 variables considered in the model included topo-
566 graphic data (elevation, slope, aspect, landform) and
567 forest structure (total basal area, proportion of pine,
568 aspen, spruce-fir basal area, height of understory
569 vegetation, and presence of seedlings). The final
570 form of the model was based on a forward selec-
571 tion process that eliminated independent variables
572 with high P -values. Coefficients from the logistic
573 regression model indicate the direction of change
574 (positive—increase, negative—decrease) required by
575 an independent variable to maximize the probability
576 of an occurrence of an active nest, given the topo-
577 graphic and environmental constraints imposed by
578 other independent variables.

579 Preliminary analysis indicated that the functional
580 form of the logistic regression model differed among
581 vegetation classes in that not all of the independent
582 variables were important in all vegetation classes. To
583 account for these differences, we added dummy vari-
584 ables to the model. After fitting the logistic regression,
585 a final model, composed of significant variables and

coefficients, was used to create a map of the probability distribution of nest locations. We standardized (Neter et al., 1985, p. 262) the regression coefficients for the logistic model to compare the relative strength of individual variables within each model, as well as across vegetation classes.

We used classification error rates to evaluate the fit of the model. To calculate classification rates, we compared the probability from the logistic regression models, a continuous variable, to a cutoff value. Each 10-m \times 10-m pixel of the NKRD was categorized into a dichotomous variable with a value of 1 or 0, representing good and poor nest locations, respectively. To determine the optimal cutoff value, we compared model results to those that would be obtained from a random process. The optimal cutoff value was selected by maximizing the improvement of model predictions over a null model of random habitat selection (i.e. maximizing the difference between the proportion of nest pixels correctly classified and the proportion of the NKRD classified as good nest habitat; Pierera and Itami, 1991; Ozesmi and Mitsch, 1997). This process considered the trade off between maximizing the correct classification of good nest habitat by selecting a lower cutoff value, and minimizing the area classified as good habitat by selecting a higher cutoff value.

Leave-one-out cross-validation (Efron and Tibshirani, 1993, p. 240) was used to generate the mean cutoff value and its associated standard deviation. This mean optimal cutoff value was used to create a grid surface showing the location of good and poor nest locations. All grid cell values over the optimal cutoff value were assigned a value of 1, while cell values less than the optimal cutoff were assigned a value of 0. The logistic regression model was also used to generate a grid surface of potential energy associated with forest structure (Eq. (14)).

3.7. Simulating the spatial distribution of goshawk nests

To simulate a point pattern of goshawk nests in a given year, the point process was conditioned on N , the total number of nests observed in the bounded region, B . Using an algorithm proposed by Ogata and Tanemura (1989), the following steps were used to simulate the two components (spatial interactions

among nests and forest structure) of the spatial distribution of goshawk nests:

- *Step 1.* Randomly locate the first nest ($t = 1$) within the bounded region B . If forest structure is taken into consideration, the location ($X_t = \{x_t, y_t \in B; t = 1\}$) of the first nest is selected proportional to $\exp[-U_1(X)]$, where $U_1(X)$ is the potential energy associated with forest structure (Eq. (14)). The nest site is selected with probability proportional to the suitability of the site, which is based on the logistic regression model (Eq. (15)). A low potential energy would indicate a good site, while a high potential energy would indicate a poor site for a nest. If forest structure is not considered in the location of nest sites, the location of the nest is chosen from a uniform distribution on the bounded region B .
 - *Step 2.* For the second and successive steps ($t = 2, \dots, N$), two additional locations are chosen: $X'_t = \{x'_t, y'_t \in B; t = 2, \dots, N\}$ and $X_t^* = \{x_t^*, y_t^* \in B; t = 2, \dots, N\}$ using the procedures outlined in *Step 1*.
 - *Step 3A.* If the spatial interaction between nests is not being considered, the total potential energies, $U'_t(X)$ and $U_t^*(X)$, associated with the two locations obtained in *Step 2* are computed (Eq. (14)) and compared. The location, X'_t or X_t^* , that minimizes the total potential energy is selected as the new location to add to the point pattern.
 - *Step 3B.* If the spatial interaction between nests is taken into consideration, the total potential energies, $U'_t(X)$ and $U_t^*(X)$, associated with the two locations obtained in *Step 2* are computed using Eq. (13). If $\min\{U'_t(X), U_t^*(X)\} < U_{t-1}(X)$, the new location, X_{t+1} is taken as $\min\{U'_t(X), U_t^*(X)\}$. If $\min\{U'_t(X), U_t^*(X)\} \geq U_{t-1}(X)$, a uniform random number, ξ , on the interval (0, 1) is computed. If ξ is less than $\exp[U_{t-1}(X) - \min\{U'_t(X), U_t^*(X)\}]$, location X_{t+1} is taken to be $\min\{U'_t(X), U_t^*(X)\}$. Otherwise, no new nest is added to the point pattern in this step.
- Steps 2 and 3 are repeated until all N nests have been located within the bounds of the population.
- *Step 4.* The last step in the simulation was to apply the Metropolis algorithm (Cressie, 1991, p. 679; Ogata and Tanemura, 1989) to adjust the initial point pattern to a state of equilibrium. This is ac-

679 completed by randomly selecting one of the N
 680 simulated nest locations $X'_t = \{x'_t, y'_t \in B; t =$
 681 $1, \dots, N\}$. Next, a new location is randomly se-
 682 lected in such a way that the coordinates $\{x'_t, y'_t\}$
 683 lie in a square with vertices at the point $x'_t \pm \delta$ and
 684 $y'_t \pm \delta$, while all other $N - 1$ nests have the same po-
 685 sition. The total potential energies associated with
 686 the two point patterns are computed and compared
 687 using the procedures described in Step 3B. If the
 688 total potential energy for the point pattern with one
 689 of the nest moved slightly is less than the poten-
 690 tial energy for the original point pattern, the nest
 691 is moved to this new location. This process is re-
 692 peated until the point pattern converges to a state
 693 of equilibrium. To ensure this convergence, δ , the
 694 maximum single step displacement allowed in pass-
 695 ing from one state to the next, was selected so as
 696 to reject one-half of the trial states (Cressie, 1991,
 697 p. 680). Other than this recommendation, no infor-
 698 mation is available in the literature on how many
 699 steps are required for convergence (Cressie, 1991,
 700 p. 680). In simulating the spatial distribution of the
 701 nests we used 78×200 Monte Carlo steps and a
 702 $\delta = 30$ m.

703 Ogata and Tanemura (1985) suggest one way to
 704 evaluate the equilibrium assumption is to examine the
 705 stationarity of the time series (t) of the total potential
 706 energy of the simulated point pattern. If we graph the
 707 change in total potential energy as a function of time,
 708 one would expect the sample mean of the time series
 709 to equal zero (Ogata and Tanemura, 1985). If a sig-
 710 nificant bias exists, this would indicate the point pro-
 711 cess is non-stationary and alternative models should
 712 be considered.

713 The goodness-of-fit of the point process model
 714 was assessed by comparing the transformed empiri-
 715 cal K -function ($\hat{L}(h) = \{\hat{K}(h)/\pi\}^{1/2}$) (Ripley, 1977),
 716 corrected for edge effect (Cressie, 1991, pp. 615–618),
 717 to the transformed K -functions from 200 simulated
 718 realizations of the model. The simulations were used
 719 in constructing confidence envelopes based on the
 720 minimum and maximum transformed K -function to
 721 test the null hypothesis of no significant differences at
 722 the $\alpha = 0.05$ level. If, for any distance, the observed
 723 transformed K -function falls above or below the con-
 724 fidence envelopes the null hypothesis is rejected at
 725 the appropriate level of significance.

726 We first evaluated the point process model describ-
 727 ing the spatial interaction between individual north-
 728 ern goshawk nests. Next, we evaluated the component
 729 describing the spatial relationship between individual
 730 nests and forest structure. Finally, we combined the
 731 two components together to simulate the spatial distri-
 732 bution of goshawk nests based on the spatial interac-
 733 tion between individual nests and forest structure. To
 734 assess the degree of agreement between the distribu-
 735 tion of predicted nest points and that of active nests,
 736 we used a chi-square goodness-of-fit to test for differ-
 737 ences in the probabilities of locating a nest between
 738 the predicted points and active nests in 1998.

739 To identify potential nest site locations, the point
 740 process model was used to simulate the locations and
 741 spatial distribution of 92 nests on the study area, repre-
 742 senting the number of territories studied between 1991
 743 and 1998. This process was repeated 50 times to gen-
 744 erate a total of 4600 potential nest locations based on
 745 the interactions between nests and forest structure. Us-
 746 ing a bandwidth of 1.5 km, a kernel estimator (Cressie,
 747 1991, pp. 597–601) was used to estimate the density
 748 of points representing potential nest locations. The re-
 749 sulting surface was standardized to a maximum value
 750 of one.

4. Results 751

4.1. Modeling nest site suitability 752

753 The mean optimum probability cut off from the
 754 logistic regression used to distinguish good from
 755 poor nest locations was $48 \pm 1.5\%$ (95% confidence
 756 intervals; S.D. = 0.008). Based on this threshold, ap-
 757 proximately one-third (410 km^2 , 33%) of the NKRD
 758 was classified as good nest habitat (Fig. 4). None
 759 of the pinyon–juniper vegetation class was classifi-
 760 ed as a good nest habitat (Table 1), while 38%
 761 (274 km^2) and 35% (36 km^2) of pure ponderosa pine
 762 and spruce-dominated sites were classified as good,
 763 respectively. Only 24% (35 km^2) of mixed-conifer
 764 sites were classified as good nest locations; whereas,
 765 48% (54 km^2) of deciduous sites provided good nest
 766 locations. Open areas obviously do not contain trees
 767 for nesting, however, in our model 14% (11 km^2)
 768 of openings (Table 1) were classified as good nest
 769 locations.

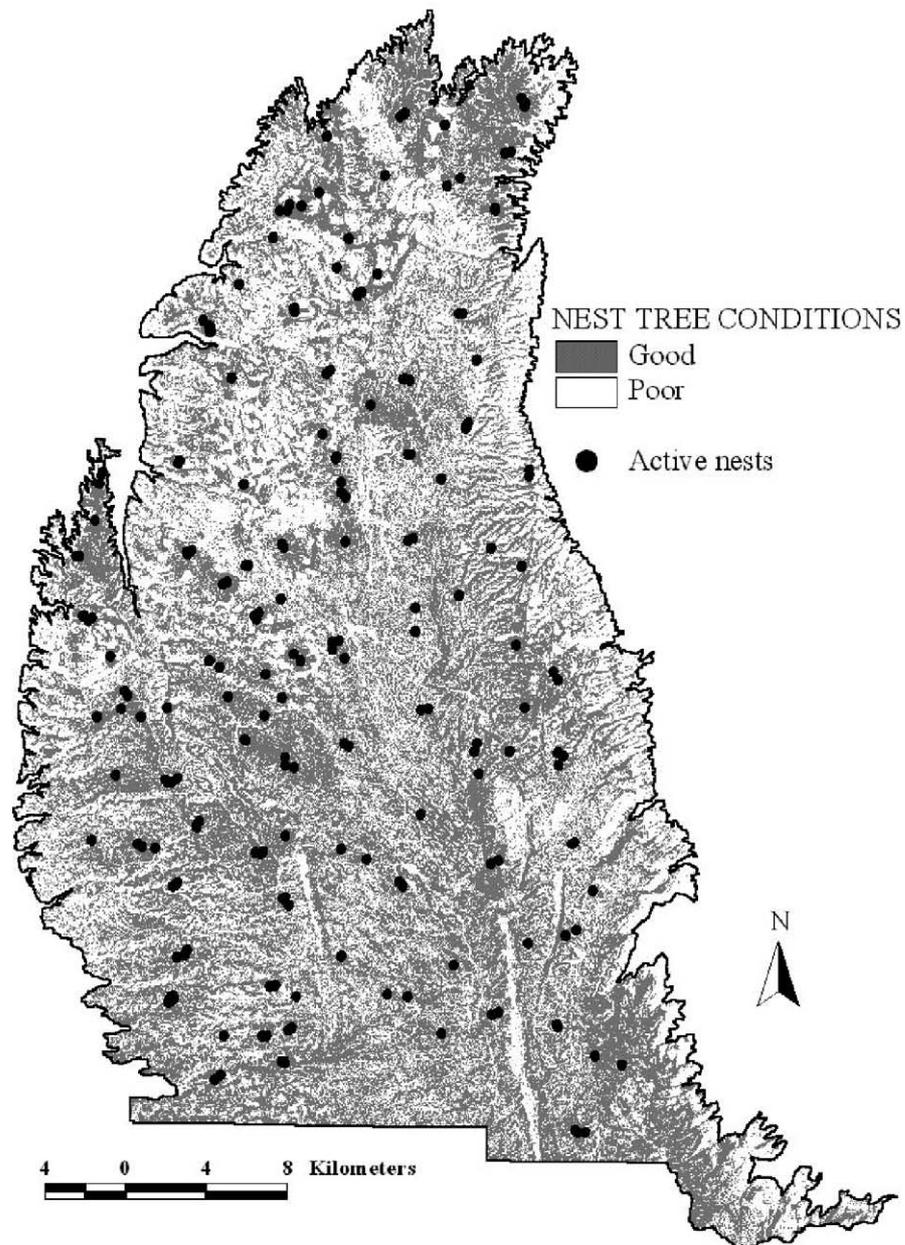


Fig. 4. Spatial distribution of estimated “good” and “poor” locations for northern goshawk nests on the North Kaibab Ranger District, Kaibab National Forest, Arizona, and all nests active between 1991 and 1998.

770 4.2. Trends in nest habitat use

771 Between 1991 and 1998, the number of active nests
 772 on the study area ranged from a low of 19 (1994) to
 773 a high of 55 (1993), representing 204 unique nest lo-

774 cations (out of 344 nest attempts) on 94 unique terri-
 775 tories (Table 2). The majority (147; 72%) of nest lo-
 776 cations, representing 51 territories, were in good nest
 777 habitat, while 57 nests (28%), representing 43 territo-
 778 ries, were in poor nest habitat (Table 3; Fig. 4). The

Table 1

Distribution of estimated good and poor northern goshawk nest habitat by vegetative class on the North Kaibab Ranger District, Arizona

Vegetation class	Good (%)	Poor (%)
Pinyon–juniper	0	100
Ponderosa pine	38	62
Mixed-conifer	24	76
Spruce-dominated mix	35	65
Deciduous-dominated mix	48	52
Opening	14	86
All vegetation classes	33	66

779 largest proportion (79%) of nests in good habitat was
780 in the ponderosa pine class. The fewest ($\leq 5\%$) nests in
781 good habitat were found in deciduous-dominated and
782 mixed-conifer forests. Of the 57 nests in poor habitat,
783 over half (54%) were also in ponderosa pine, while
784 almost a third (30%) were in the mixed-conifer class.
785 Regardless of vegetation class, however, nearly 80%
786 (45 of 57) of nests in poor sites were found within
787 10 m of a good site.

4.3. Nest habitat

788

789 Important variables from the logistic regression
790 model and their standardized coefficients (Table 4),
791 which discriminated between good and poor nest
792 site locations, varied with vegetation class (Table 5).
793 In ponderosa pine, the likelihood that a stand con-
794 tained a nest improved with increasing total basal
795 area (above 29 m²/ha), but smaller proportions of
796 spruce-fir basal area ($< 5.5\%$) and, especially, aspen
797 basal area ($< 7.9\%$). Denser canopy closures, flatter
798 slopes, and understory vegetation taller than 0.5 m
799 also improved the probability of a nest location. In
800 the mixed-conifer zone, the likelihood of observing a
801 nest was greater on steeper ($> 8\%$) slopes with easterly
802 exposure, and in drainages, particularly where smaller
803 proportions of spruce and fir, but greater proportions
804 of aspen basal area, occur. Elevations lower than ap-
805 proximately 2600 m a.l.s., understory vegetation taller
806 than 0.5 m, dense canopy closures and, in particular,
807 seedlings and saplings also improved the likelihood
for nest habitat in the mixed-conifer forest type. In

Table 2

Total number of territories and active northern goshawk nests between 1991 and 1998 above 2182 m in elevation on the North Kaibab Ranger District, Arizona

	Year								Total
	1991	1992	1993	1994	1995	1996	1997	1998	
Total territories monitored	36	58	72	87	95	102	105	105	660
New territories with active nests	36	21	13	3	10	8	0	4	94
Active nests	35	52	55	19	48	42	30	53	344
New active alternate nests	35	37	33	9	29	21	15	25	204

Table 3

Number of active nests between 1991 and 1998 by estimated suitability (good, poor) of nest locations and vegetative class on the North Kaibab Ranger District, Arizona

Vegetation class	Good		Poor		Total number of nests
	Number of nests	%	Number of nests	%	
Pinyon–juniper	0	0	0	0	0
Ponderosa pine	116	79	31	54	147
Mixed-conifer	8	5	17	30	25
Spruce-dominated mix	17	12	5	9	22
Deciduous-dominated mix	6	4	4	7	10
Openings	0	0	0	0	0
Total	147	100	57	100	204

Table 4

Standardized regression coefficients for variables that maximize the likelihood of a northern goshawk nest occurring in a vegetative class on the North Kaibab Ranger District, Arizona

Variable	Vegetation class					
	Pinyon–juniper	Ponderosa pine	Mixed-conifer	Spruce-dominated mix	Deciduous-dominated mix	Openings
Aspect	–	–	–0.082	–0.172	0.570	–
Slope (%)	–0.373	–0.044	0.041	0.007	0.653	–0.001
Elevation (m)	–	–	–0.016	0.077	–	–0.052
Landform	–	–	0.067	–0.083	–0.324	–
Total BA ^a (m ² /ha)	0.050	0.102	0.116	–0.040	0.112	0.032
Ponderosa pine BA ^b	–	–	–	0.689	–	–
Spruce-fir BA ^b	–0.051	–0.042	–0.096	–	0.639	–0.067
Aspen BA ^b	0.000	–0.109	0.076	–	–0.236	0.020
Canopy ^c	–0.004	0.003	0.002	0.002	–0.002	–0.001
Understory height (m)	0.053	0.046	0.039	–0.192	–0.486	0.062
Seedlings ^d	0.062	0.061	0.128	0.091	0.039	0.053

The magnitude and direction of the coefficients (positive—increase, negative—decrease) are comparable within and between models.

^a Basal area.

^b Proportion of total BA (m²/ha).

^c Proportion of canopy closure.

^d Presence or absence.

808 spruce-dominated areas, higher nest-use was associ-
 809 ated with less total basal area—although proportions
 810 of ponderosa pine greater than 23%, particularly con-
 811 current with shorter (<7 m) understory heights—and
 812 somewhat greater canopy closure. Flatter, east-facing

slopes, higher elevations than approximately 2680 m, 813
 and gradual ridges on the landscape also increase the 814
 likelihood for locating a nest in spruce-dominated 815
 landscapes. In deciduous-dominated forests, nest site 816
 use was enhanced by the presence of ridges and, espe-

Table 5

Means for variables that maximize the likelihood of a northern goshawk nest occurring in a vegetative class on the North Kaibab Ranger District, Arizona

Variable	Vegetation class					
	Pinyon–juniper	Ponderosa pine	Mixed-conifer	Spruce-dominated mix	Deciduous-dominated mix	Openings
Aspect	–	–	181	155	129	–
Slope (%)	18	6	8	7	9	7
Elevation (m)	–	–	2605	2682	–	2490
Landform	–	–	0.002	–0.046	0.327	–
Total BA ^a (m ² /ha)	17	29	39	36	30	2
Ponderosa pine BA ^b	–	–	–	0.228	–	–
Spruce-fir BA ^b	0.068	0.055	0.706	–	0.442	0.052
Aspen BA ^b	0.000	0.079	0.138	–	0.825	0.087
Canopy ^c	0.800	0.931	1.035	1.038	1.057	0.267
Understory height (m)	0.947	0.506	0.499	0.682	0.592	0.772
Seedlings ^d	0.371	0.639	0.887	0.944	0.897	0.222

^a Basal area.

^b Proportion of total BA (m²/ha).

^c Proportion of canopy closure.

^d Presence or absence.

817 cially, steeper (>9%) slopes with south or south-west
818 facing aspects, shorter (<6 m) understory vegetation,
819 and greater amounts of total basal area, including
820 larger proportions (>44%) of spruce-fir basal area,
821 but lower proportions (<82%) of aspen basal area.
822 Lower canopy closures, more typical of spruce-fir
823 than of aspen, also improve the potential for nesting.
824 It follows that openings, which are devoid of trees, re-
825 quire greater amounts of total basal area than 2 m²/ha
826 to improve their potential for nest site use. Greater
827 amounts of aspen, which is generally a seral species
828 in openings following a disturbance, increase nest
829 use potential in particular. Seedlings, saplings, and
830 taller understory vegetation are also favored. Accord-
831 ing to our logistic model, none of the pinyon–juniper
832 vegetation class was considered “good” nest habitat.
833 Nonetheless, we derived coefficients for the variables
834 that would maximize the likelihood of a nest occur-
835 rence in this forest type. These conditions included
836 flatter slopes (<18%) and the presence of seedlings
837 and saplings, greater total basal area (>17 m²/ha), but
838 smaller proportions (<7%) of spruce-fir basal area,
839 and a slightly more open (<80%) canopy. Overall, our
840 model suggests that the presence of seedlings and/or
841 saplings improves nest habitat in all vegetation classes.

4.4. Simulating the spatial distribution of nests

842

843 The transformed K -function (Fig. 5) of the spa-
844 tial distribution of individual goshawk nests ($N =$
845 27) in the rectangular region B shows some terri-
846 toriality as the empirical K -function extends below
847 the lower simulation envelope for distances less than
848 2 km. The minimum distance observed between active
849 nests in 1998 was 1.6 km. This indicates that there are
850 fewer pairs of nests within a 2-km distance than ex-
851 pected if the nests were randomly distributed, and that
852 those nests were regularly distributed. At distances
853 greater than 2 km, the empirical K -function is con-
854 tained within the simulation envelopes, indicating that
855 the spatial distribution of goshawk nests does not dif-
856 fer significantly from a random spatial pattern. The
857 Cramér–von Mises goodness-of-fit statistic also indi-
858 cated some non-randomness in the spatial distribution
859 of goshawk nests (Table 6). The P -value associated
860 with this test was ≤ 0.14 for all distances ≤ 16 km. The
861 strongest degree of non-randomness ($P < 0.05$) was
862 observed for distances less than 6 km.

863 When the Gibbsian pairwise potential model was
864 fit to the nest point data, model PF2 ($\hat{\alpha} = 0.005204$,
 $\hat{\beta} = 0.005923$) (Fig. 6) was selected as the best fit-

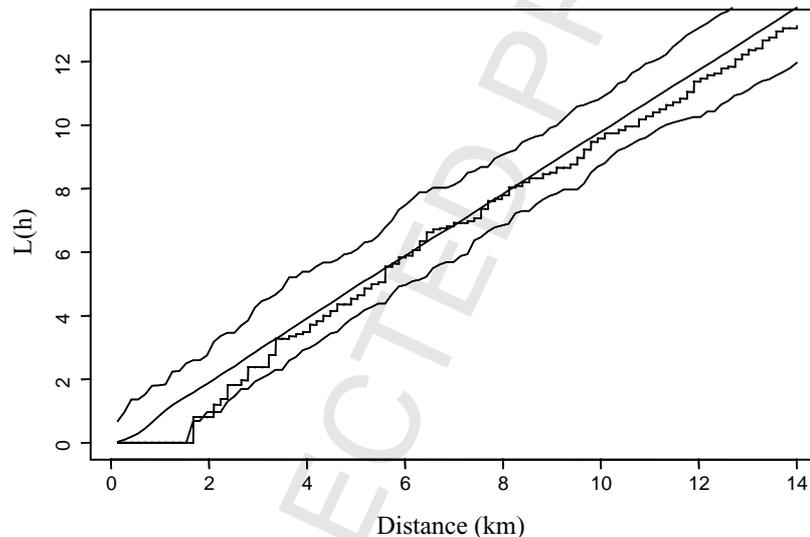


Fig. 5. Plot of the transformed K -function, $L(h) = [K(h)/\pi]^{1/2}$, against distance h , used to model the spatial arrangement of individual northern goshawk nests on the bounded region (B) on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The stair-step line represents the empirical K -function calculated from the data; continuous lines represent the upper, average, and lower 99% simulation envelopes for 200 realizations of a spatial Poisson process.

Table 6

Results of the Cramér–von Mises goodness-of-fit test used to test the null hypothesis that northern goshawk nests in 1998 were randomly distributed on the North Kaibab Ranger District, Arizona

Distance (km)	Test statistic	<i>P</i> -value
2	282.25	0.00
3	238.38	0.03
4	195.17	0.00
5	163.32	0.01
6	136.43	0.02
7	117.68	0.06
8	109.72	0.13
9	95.31	0.13
10	98.55	0.10
11	96.42	0.09
12	101.12	0.03
13	104.97	0.13
14	107.94	0.11
15	110.31	0.14
16	119.35	0.08

ting model based on the AIC. The shape of the potential function suggests that individual nesting pairs of goshawks have a repulsive tendency toward one another and that the territorial effects between individual pairs decrease with increasing distance between nests (i.e. soft-core model). The point at which the potential energy approaches zero (≈ 20 km) provides an estimate of the maximum zone (circular area) of territoriality around individual nests. This result corroborates the above-mentioned results.

The transformed empirical *K*-function for the component of the point process model that describes the spatial interaction between individual nests (Fig. 7a) is contained within the bounds of the simulation intervals indicating the model provides a good fit to the data. In the range of 5.5–9.5 km, the point process model shows a more regular pattern than observed in the data. Territories defended by goshawks may be irregular in shape, especially in years when neighboring pairs are not breeding, and their nests may be located near the edge of their territories. Thus, at coarser scales there may be a tendency for some type of clustering of nests. In contrast, the model assumes the nests are at the center of their territories and exhibit an equal territorial force in all directions, resulting in a more regular pattern at all scales. The fact that the empirical *K*-function is contained within the simulation envelopes suggest the following two hypotheses: (1) the distribution of goshawk nests are spatially independent of forest structure; and (2) there is enough available habitat for nests on the study area as to not limit the spatial distribution of individual goshawk nests.

Except for distances less than 2 km, the transformed empirical *K*-function for the forest structure component of the point process model (Fig. 7b) is contained within the bounds of the simulation intervals. This graph looks similar to the one obtained when we tested for CSR (Fig. 5), suggesting that

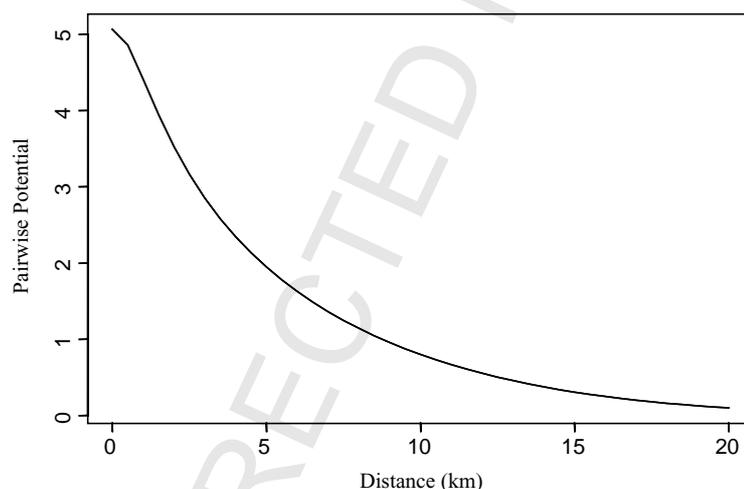


Fig. 6. Plot of the fitted pairwise potential model (PF2) for individual northern goshawk nests on the bounded region (*B*) on the North Kaibab Ranger District, Kaibab National Forest, Arizona.

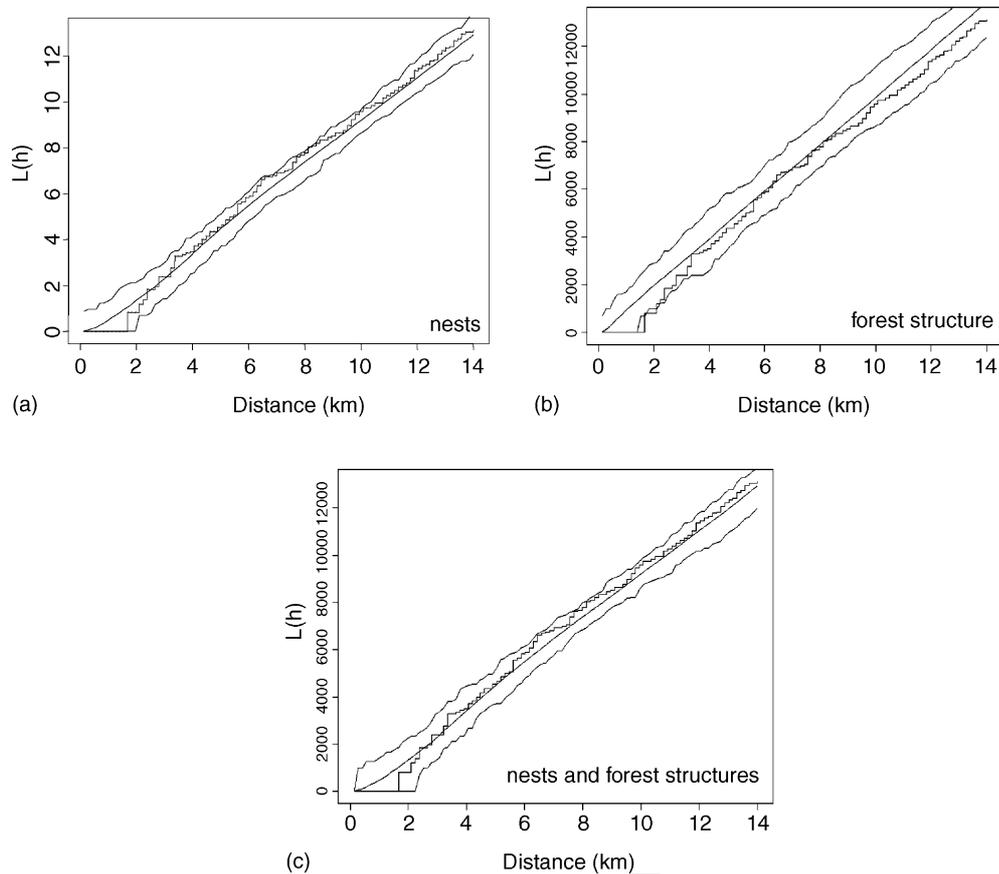


Fig. 7. Plot of the transformed K -function, $L(h) = [K(h)/\pi]^{1/2}$, against distance h , used to model the spatial arrangement of individual northern goshawk nests on the study area on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The stair-step line represents the empirical K -function calculated from the data and the continuous lines represent the upper, average, and lower 99% simulation envelopes for 200 realizations of the (a) nest component of the point process model, (b) forest component of the point process model, (c) point process model that takes into consideration the territoriality between individual active nests and forest structure.

903 if we allocate nests using the potential energy as-
 904 sociated with forest structure we generate a pattern
 905 similar to that of a random one. This result supports
 906 the second hypothesis that the current availability of
 907 good nest locations on the study area is not a factor
 908 limiting the spatial distribution of active goshawk
 909 nests.

910 The transformed empirical K -function for the com-
 911 plete model (Fig. 7c) is contained within the bounds
 912 of the simulation intervals indicating that the spatial
 913 model is capable of describing the distribution of nests
 914 on the study area, and in turn, provides a measure
 915 of the spatial dependency among individual nests and
 916 forest structure. Realization of the final model allows

917 us to predict the location of 27 nest points within
 918 the bounded region B (Fig. 8) and 96 nest points on
 919 the entire KNF (Fig. 9). The distribution of nest site
 920 probabilities associated with the predicted points de-
 921 picted in Fig. 9 did not differ ($\chi^2 = 11.14$, d.f. = 9,
 922 P -value = 0.266) from the nest site probabilities as-
 923 sociated with active nests in 1998 on the study area
 924 (Table 7).

925 The estimated density of potential nest locations
 926 based on 50 simulations of the point process model and
 927 a kernel bandwidth of 1.5 km (Fig. 10) suggests that
 928 the spatial distribution of nest sites is non-stationary
 929 (i.e. densities shift with the number of simulations).
 930 Consequently, there is a trend of increasing poten-

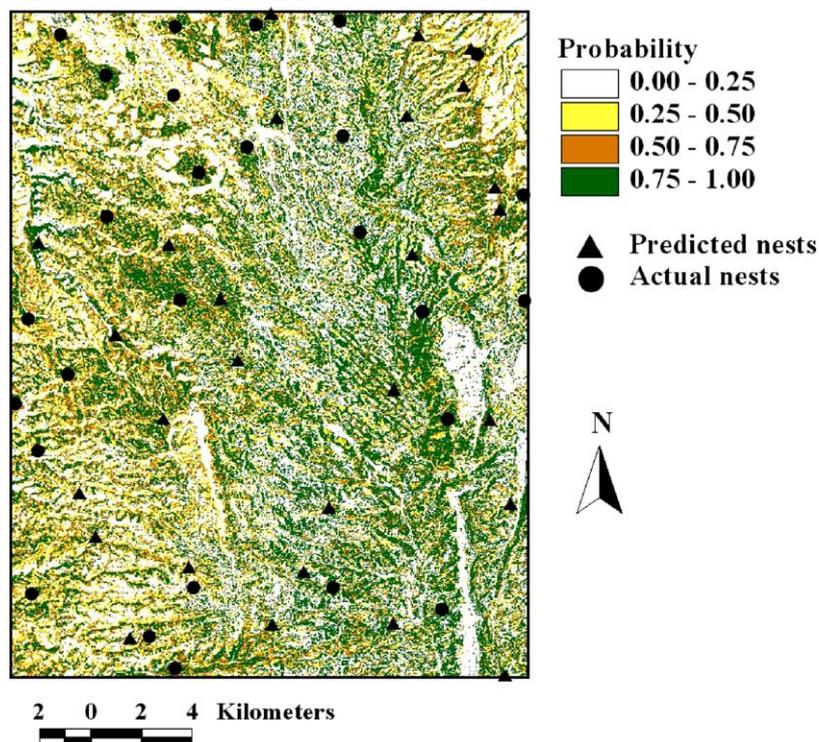


Fig. 8. Realization of the point process model (▲) that takes into consideration the territoriality between individual northern goshawk nests and forest structure on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The locations of 27 active northern goshawk nests (●) used in fitting the model are plotted for comparison. The point patterns are overlaid on a surface showing the probability of finding a northern goshawk nest within the bounded region (B) on the study area associated with forest structure. Areas with a low probability (poor nest areas) are lighter in color and areas with a high probability (good nest areas) are darker in color.

931 tial nest site density from the center of the study
 932 area outward. The edges of the study area tend to
 933 have a higher likelihood of nest sites than the interior
 934 portion, in part, due to the nonexistence of territories
 935 (i.e. territorial influence) outside the study area
 936 boundary to the north, east, and west, and to the exclusion
 937 of territories in the Grand Canyon National Park.
 938 Notably, the model suggests that there should be nests
 939 in the southeastern part of the study area. However,
 940 this area is dominated by dense aspen habitat unlikely
 941 to support nesting goshawk, as well as a closed under-
 942 story that would most likely prohibit foraging goshawks
 943 from accessing prey (R.T. Reynolds, personal observa-
 944 tion). Overall, though, an overlay of the locations of all
 945 active nests observed from 1991 to 2002, shows a high
 946 degree of correspondence between the potential nest site
 947 density plot and active nests.
 948

5. Discussion

949

950 Spatial statistics have not been used to their fullest
 951 potential in animal ecology due to a generally poor un-
 952 derstanding of these statistical methods. Recent eco-
 953 logical models that predict the distribution and abun-
 954 dance of wildlife species are derived from GLM or
 955 GAM that relate spatially-explicit response variables
 956 (distribution or density) to spatially referenced covari-
 957 ates (habitat measurements) (James and McCulloch,
 958 2002; Lehmann et al., 2002). For example, logistic re-
 959 gression is used to predict the suitability of habitat or
 960 the probability of a species' occurrence (Pearce and
 961 Ferrier, 2000; Guisan and Zimmermann, 2000). Au-
 962 tologistic models, on the other hand, are used to ac-
 963 count for spatial autocorrelation among sampled pop-
 964 ulations of species that respond in a clustered or ag-
 965 gregated manner (Augustin et al., 1996; Austin, 2002).

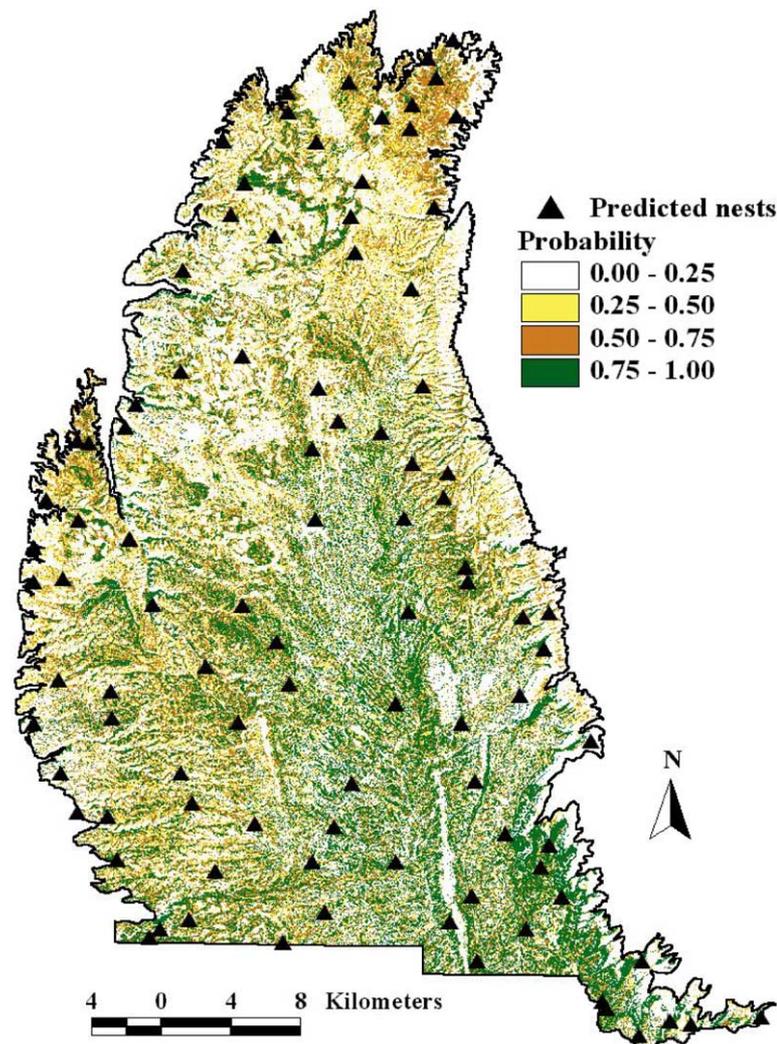


Fig. 9. Realization of the point process model (▲) that takes into consideration the territoriality between northern goshawk nests and forest structure on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The predicted point pattern of nests is overlaid on a surface showing the probability associated with forest structure of finding a northern goshawk nest within the study area. Areas with a low probability (poor nest areas) are lighter in color and areas with a high probability (good nest areas) are darker in color. The probabilities associated with each simulated point do not differ ($\chi^2 = 11.14$, d.f. = 9, P -value = 0.266) from those of actual nests.

966 Spatial covariates (typically habitat attributes) used in
 967 these models are assumed to be biologically meaning-
 968 ful. However, model prediction errors are generated,
 969 in part, by a failure to incorporate behavioral aspects
 970 (such as competition) into the model (Austin, 2002;
 971 Pearce et al., 2002). While these techniques represent
 972 significant progress in modeling the distribution and
 973 abundance of wildlife species, they do not account

974 for inter- or intra-specific competition. These models, 974
 975 therefore, may not provide accurate representations of 975
 976 the biological factors governing aspects of abundance 976
 977 (Keitt et al., 2002). 977

978 We present a flexible point process model that de- 978
 979 scribes the spatial dependency between the location of 979
 980 active goshawk nests and forest structure. The model 980
 981 assumes that individual nests are distributed accord- 981

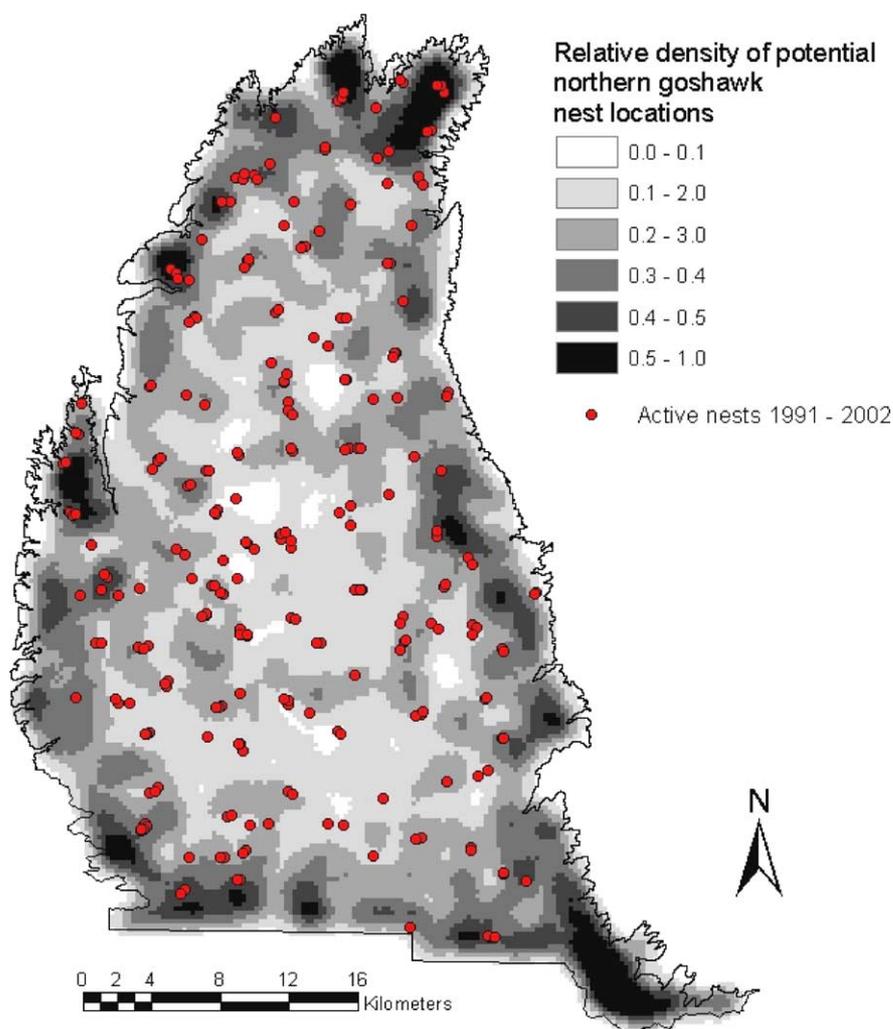


Fig. 10. Standardized nonparametric kernel estimate of the density of potential northern goshawk nests on the North Kaibab Ranger District, Kaibab National Forest, Arizona using a 1.5km kernel. Density estimates were based on 50 realizations of the point process model that take into consideration the territoriality between individual northern goshawk nests and forest structure. Overlaid on the figure are the locations (●) of all goshawk nests observed from 1991 to 2002.

982 ing to the potential energy associated with the struc-
 983 ture of the forest and a conspecific-competitive effect
 984 (territoriality).

985 In our goshawk study, it appeared that suitable nest
 986 habitat was not limiting the distribution and abundance
 987 of goshawks on the NKRD. Instead, territoriality,
 988 and what appeared to be non-compressible territories,
 989 limited the distribution and abundance of the nesting
 990 population. Within territories, choices of nest loca-
 991 tions appeared to be limited by the availability of sites

with “good” nest habitat (suitable forest structures
 and topography; see Reynolds et al., 1992). Territory
 size and ultimately density, on the other hand, proba-
 bly reflected the amount of suitable goshawk foraging
 habitat and the abundance, distribution, and accessi-
 bility of prey within territories (Newton et al., 1977;
 Nilsson et al., 1982; Kenward and Widén, 1989;
 Widén, 1997; Kenward et al., 2001).

Annual nest locations were regularly distributed
 with a minimum of 1.6km between active nests.

Table 7

Distribution of probabilities of finding a northern goshawk nest associated with predicted and observed (1998) nest points on the North Kaibab Ranger District, Arizona

Observed nests		Predicted nests	
Probability	Frequency	Probability	Frequency
0.0–0.1	9	0.0–0.1	11
0.1–0.2	5	0.1–0.2	3
0.2–0.3	5	0.2–0.3	6
0.3–0.4	11	0.3–0.4	8
0.4–0.5	12	0.4–0.5	9
0.5–0.6	12	0.5–0.6	11
0.6–0.7	7	0.6–0.7	13
0.7–0.8	7	0.7–0.8	11
0.8–0.9	11	0.8–0.9	12
0.9–1.0	17	0.9–1.0	14

1002 Although goshawks need only a small patch (about
1003 0.01–0.10 km²) of suitable habitat to nest, the
1004 “quality” of those sites (judged by annual rate of
1005 egg laying and number of young produced) should,
1006 in part, be determined by the suitability of surround-
1007 ing habitat for supporting populations of diverse
1008 prey species and providing foraging opportunities for
1009 goshawks (Reynolds et al., 1992; Widén, 1997). Al-
1010 though the “quality” of nest sites was not used in this
1011 study, nest site quality varied across the study area
1012 (Joy, 2002, pp. 153–219). Nevertheless, degradation
1013 of forest structure in large areas by forest manage-
1014 ment or natural disturbances may reduce the quality
1015 of nest habitat, thereby affecting the distribution of
1016 goshawk territories in our model.

1017 In our final model, the locations of active goshawk
1018 nests appeared to be the result of territoriality. How-
1019 ever, the distribution of good and poor potential habi-
1020 tat, based on forest structure, played an important role
1021 in nest location within territories. The within-territory
1022 relationship to forest structure may reflect past for-
1023 est management on the NKR. While many forests
1024 in the southwest received heavy railroad logging in
1025 the late-1800 and early 1990s, the Kaibab Plateau,
1026 because of its isolation by the Grand Canyon, was
1027 not railroad-logged during this period (Pearson, 1950).
1028 Management on the NKR since the 1960s has been
1029 variable; some areas have been heavily harvested (i.e.
1030 seed tree, shelterwood cuts, clearcuts), while others
1031 received less tree cutting (i.e. thinning, individual tree
1032 selection). Areas heavily harvested between 1958 and

1998 generally contain more low quality nest habitat 1033
(74% of 114 km²). In contrast, areas within 1200-m 1034
radii of active nests, which contain lesser amounts of 1035
low quality nest habitat (62% of 114 km²). With the 1036
implementation of management to enhance goshawk 1037
nest and foraging habitats (Reynolds et al., 1992), the 1038
structure of the forest should become more suitable 1039
for both goshawks and their prey species. 1040

The varying importance and direction (increase, 1041
decrease) of forest structural components based on 1042
logistic regression coefficients within each vegetation 1043
class (Table 4) predict identify structural conditions 1044
that increased a site’s potential to contain a goshawk 1045
nest. Increased total basal area in all vegetation 1046
classes, except the spruce-dominated type, improved 1047
nest habitat. Less spruce-fir and aspen in ponderosa 1048
pine forests, greater proportions of ponderosa pine 1049
trees in spruce-dominated forests, less spruce and 1050
fir trees and more aspen in the mixed-conifer forest, 1051
and less aspen, but more spruce and fir trees in the 1052
deciduous-dominated forest increase a site’s poten- 1053
tial. In ponderosa pine forests, more spruce and/or fir 1054
trees increases the density of smaller trees, restricting 1055
a goshawk’s access to its nest; whereas, more aspen 1056
(which typically have high, thin crowns) might de- 1057
crease the vegetation cover at or near nests, especially 1058
prior to leaf-out. In spruce-dominated habitat, pon- 1059
derosa pine crowns provide large branches for nest 1060
substrate, easier access to the nest, and would provide 1061
more cover above a nest. Because mixed-conifer for- 1062
est is typically dense in both overstory and understory 1063
(S.M. Joy, personal observation), increased amounts 1064
of aspen basal area in a mixed-conifer site improves 1065
nest site habitat quality by opening the understories, 1066
providing large open crowns for nest placement and 1067
easier access to nests. In large openings created by 1068
management or natural disturbance, our model sug- 1069
gests the obvious—regenerating these areas restores 1070
the potential of these sites to contain nests. 1071

Nest habitat is enhanced by greater canopy closure 1072
and less steep slopes in ponderosa pine forests. In the 1073
deciduous-dominated forest type, less canopy closure, 1074
greater basal area of ponderosa pine, and steeper, 1075
southeast-facing slopes associated with increasing 1076
gradient of convexity improves nest habitat. Steeper 1077
slopes associated with drainages at elevations below 1078
2600 m, easterly-facing exposures, and dense canopy 1079
closure, improve nest habitat within the mixed-conifer 1080

1081 forest. Nests in mixed-conifer forests are typically
1082 found in trees (usually ponderosa pine) on steep
1083 slopes. At lower elevations, east-facing slopes in
1084 drainages have more ponderosa pine trees or aspen,
1085 which provides greater canopy coverage as well as a
1086 greater number of useable nest trees and perhaps limits
1087 the amount of fir regeneration. The habitat character-
1088 istics that create good nest sites in spruce-dominated
1089 forests—east-facing exposures with a slightly convex
1090 landscape—would most likely enhance the growth of
1091 more spruce and fir. Pinyon–juniper, which tends to
1092 grow on steep, dry, west-facing slopes above 2182 m
1093 on NKRD improved nest habitat only on flatter slopes
1094 and on sites with less canopy closure. Although
1095 goshawk nests are not found in pinyon–juniper forests
1096 on the study area, they do occur in narrow stands
1097 (stringers) of ponderosa pine in drainages that ex-
1098 tend into the pinyon–juniper zone (S.M. Joy, personal
1099 observation). These stringers of ponderosa pine can
1100 provide cooler sites for nesting.

1101 Our model suggests that the presence of seedlings
1102 and/or saplings “improves” nest habitat in all vege-
1103 tation classes. However, the nature of tree regenera-
1104 tion in actual nest areas varied widely. In some areas,
1105 seedlings/saplings were small and few, and did not
1106 impose a physical or visual barrier for nesting hawks.
1107 However, as saplings increase in size and density, they
1108 likely hinder goshawk movements to and from nest
1109 trees. Regardless, the presence or absence of seedlings
1110 and saplings alone is insufficient to provide a biolog-
1111 ically meaningful index of nest site potential. Shrubs
1112 and herbaceous understory height may also be a poor
1113 predictor for similar reasons.

1114 Although the majority (86%) of openings on the
1115 study area were classified as poor nesting habitat,
1116 some openings (14%) were classified as good habitat.
1117 Within ponderosa pine and mixed-conifer forests on
1118 the NKRD, small (10-m × 10-m) openings are com-
1119 mon. These small openings may represent some of
1120 the 14% that fell in good nest habitat; whereas, some
1121 openings classified as good nest habitat may be classi-
1122 fication errors attributed to the “open” vegetation class.
1123 Openings contained the highest (23%) classification
1124 error rate of all vegetation classes (Joy et al., 2003).

1125 Between 1991 and 1998, 57 out of 204 active nests
1126 were in “poor” nest habitat. Of the 80% (45) were
1127 found within 10 m of a “good” nest site, regardless
1128 of vegetation class. The classification of these nest

1129 locations as poor might have been due to errors in
1130 the mapping of nest trees or registration of the Land-
1131 sat information. Mapping errors lower the significance
1132 of the logistic regression model, indicating that good
1133 nest locations are more randomly distributed (Stoms
1134 et al., 1992) and decrease our ability to discriminate
1135 nest sites from random sites. However, we believe the
1136 majority of our nests were mapped to within 3 m of
1137 their actual locations. Alternatively, if the spatial res-
1138 olution of our models did not capture the geographic
1139 scale at which goshawks choose nest trees (e.g. if nest
1140 trees were selected based on local prey availability),
1141 we might also expect more nests to be in poor sites.
1142 Furthermore, adult territorial goshawks not nesting in
1143 one or more years likely introduced spaces into the
1144 distribution of territories and nests, and errors in our
1145 classification of good and poor nesting habitat. We be-
1146 lieve that territorial interactions (Ozesmi and Mitsch,
1147 1997) among breeding goshawks, as well as potential
1148 interactions with other raptors (Janes, 1984) and the
1149 lack of good sites in some territories, explain why not
1150 all of the active nests were located in good sites.

1151 Treating forest structural components as one con-
1152 tinuous variable in the model allowed the introduction
1153 of environmental heterogeneity into the point process
1154 model. Including environmental heterogeneity, in turn,
1155 allowed the spatial interaction between goshawk pairs
1156 at nests, both locally and regionally, to be modeled.
1157 Such a model is useful in simulating the effects that
1158 changes in a forest have on the spatial dynamics of a
1159 goshawk population. This is accomplished by system-
1160 atically changing the potential energy associated with
1161 forest structure and observing how change influences
1162 the spatial distribution of goshawk nests. As some
1163 nest sites become unsuitable because of disturbance,
1164 goshawks may move to an alternate nest within their
1165 territory. The location of alternate nests within territo-
1166 ries depends on the availability of sites. Our model also
1167 provided information on the potential of goshawk oc-
1168 cupancy of a forest area. Moreover, when the demog-
1169 raphy of a goshawk population is incorporated into the
1170 point process model, it should be possible to study the
1171 spatio-temporal behavior of the goshawk population
1172 as influenced by forest management activities.

1173 Such a model should benefit researchers and man-
1174 agers interested in ecosystem processes by providing a
1175 better understanding of the influence that coarse- and
1176 fine-scale spatial variability have on the abundance and

1177 productivity of goshawk populations. The Gibbsian
1178 pairwise potential model used here accounted for the
1179 response of northern goshawks to their environment,
1180 as well as the effects of conspecific-competitive in-
1181 teractions (territoriality). Knowledge of nest locations
1182 based on territorial spacing, as well as environmen-
1183 tal variables, should be a priority for habitat managers
1184 because managers need to know more than the prob-
1185 ability of a nest being in a particular location—they
1186 also need to know how individuals or species interact
1187 behaviorally to influence those locations.

1188 While our specific model may not be applicable to
1189 all forests because it was based on population-level
1190 data, models can be developed for alternate areas us-
1191 ing sample data (i.e. incomplete data on a popula-
1192 tion). The Takacs–Fiksel method could be used to es-
1193 timate the parameters of the pair-potential functions
1194 using data collected through sample field observa-
1195 tions (Tomppo, 1986). Apart from the Takacs–Fiksel
1196 method (based on a step function), no other estima-
1197 tion methods have been applied to field observations.
1198 Also, the pseudo-likelihood estimation methods, em-
1199 ployed in this paper, coincide with the Takacs–Fiksel
1200 method depending on the pair-potential function used
1201 (Diggle et al., 1992). Hence, one can assume that the
1202 pseudo-likelihood method is also applicable to field
1203 observations. It is possible, therefore, to develop mod-
1204 els similar to the one presented in this paper for other
1205 forests or using sample data. Such models could be
1206 used to identify potential nest site locations, as well
1207 as identify areas that should have a high priority for
1208 management under the goshawk management recom-
1209 mendations (Reynolds et al., 1992).

1210 Austin (2002) suggested that ecological processes
1211 be incorporated into statistical models to produce
1212 more robust predictions and equations with more ex-
1213 planatory power. Austin (2002, p. 103) states that,
1214 “Current (analytical) techniques need not be limited
1215 to static equilibrium situations . . .” Our approach
1216 to modeling the spatial dynamics of an individual
1217 species with their habitat is at the leading edge of
1218 ecological modeling. Furthermore, our modeling
1219 approach can be used in a variety of applications
1220 and study areas once inter- or intra-specific interac-
1221 tions and species–environment interactions have been
1222 modeled. Inferences from the model generated here,
1223 however, should not be made beyond the scope of our
1224 study area. In areas where goshawks may occur at

1225 lower densities than on the NKR, where nest spac-
1226 ing might be irregular, or where habitat data are at a
1227 coarser resolution, a new point process model should
1228 be developed.

Uncited reference

Kenward (1982).

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